Gary Lane

July 15 - 16, 1989

WORKSHOP ON FOSSIL CRINOID
WORKSHOP ON FOSSIL CRINOIDS

Introduction

The Workshop on Fossil Crinoids at the 28th International Geological Congress is designed to bring scientists interested in and engaged in studies of the Crinoidea together for loosely structured discussions of many aspects of morphology, evolution, and paleoecology of fossil crinoids.

Special thanks for logistical support for this workshop go to Dr. Frederick J. Collier, of the Department of Paleobiology, Natural History Museum, Smithsonian Institution.

Schedule

July 15

9:00    Welcome by Frederick J. Collier

9:20    Introduction to the Workshop, Thomas W. Broadhead

Theme - Morphology and Evolution

"What is Progress in the Crinoidea?, William I. Ausich


"Were Many Paleozoic Crinoids Facultative Eleutherozoans", Gary Lane

"Growth Rate of Stalk of Metacrinus rotundus Carpenter and its functional significance", Tatsuo Oji

"Ecogenesis of Post-Paleozoic Crinoids", V.G. Klikushin

"Relationship of Anal Sac Support and Arms", Thomas W. Broadhead

10:00   Coffee Break for 15 minutes (time approximate)

11:15-1:00 Lunch Break at one of the public cafeterias on the Mall

Theme - Morphology and Evolution

Other topics

2:30    Coffee Break for 15 minutes (time approximate)
Theme - Evolution and Classification

"Is the Present Classification of the Class Crinoidea Satisfactory at the Family Level and at Higher Levels?", Gary Lane

5:00 Conclusion for the Day

July 16

9:00 Resume discussions on Evolution and Classification

"The Relationships (or Nonrelationships) of Reticocrinus Billings, 1859, Thomas E. Guensburg

"Are the Cladids a Single, Coherent Evolutionary Unit?", Gary Lane

"How did the Comatulid Crinoids Evolve?", Gary Lane

Other topics

10:00 Coffee Break for 15 minutes (time approximate)

11:00-1:00 Brunch at the Museum

Theme - Paleoecology and Taphonomy

"How Did Crinoids Compete During Their Growth Cycle", Gary Lane

"Were There Deep Water Stemmed Crinoids in the Paleozoic", Gary Lane

"Trophic Structure of a Middle Ordovician Echinoderm Community", James C. Brower

Other topics

2:30 Coffee Break for 15 minutes (time approximate)

5:00 Concluding Remarks
WHAT IS PROGRESS IN THE CRINOIDEA?

William I. Ausich
Department of Geology & Mineralogy
The Ohio State University
Columbus, Ohio 43210

Major evolutionary trends among the Crinoidea have traditionally been defined by describing a morphological vector between typical Ordovician crinoids and typical Permian or post-Paleozoic crinoids. Examples of major evolutionary trends identified in this manner include the following: 1, reduction and eventual elimination of fixed brachials, interradial, and anal plates from the aboral cup; 2, increase in the number of arms and the complexity of the arm branching system; 3, modification of high conical aboral cups to low, bowl-shaped cups; and the attainment of perfect pentameral symmetry of the crown (Moore & Laudon, 1943; Moore, 1950; Moore, 1952; among others). These evolutionary trends have been important in the evolutionary history of crinoids. However, their importance has been overstated, as they have come to be regarded as a vector of progress from primitive to advanced -- from inefficient to efficient, from bad to good.

Rather than representing progress, in the sense of bad to good, these and other evolutionary trends are simply the product of available options due to construction constraints that limited the morphological pathways for microevolutionary modifications in
crinoids. Additional important morphological trends include some that are exactly the opposite of the traditional trends, and this feature of the evolution of crinoids needs more emphasis than given in the Treatise (Moore & Teichert, 1978). For example, the addition of fixed brachials and/or interradials into the calyx occurred in all subclasses. Calyx designs identified by Ausich, (1988) are interpreted as adaptive peaks. Evolutionary modification between these various designs was accomplished via both the traditional trends and the reverse of traditional trends. Addition of fixed interradials is regarded as a derived feature among the camerates Xenocrinidae and Reteocrinidae (Brower, 1974; Ubaghs, 1978). Addition of calyx plates is a diagnostic trend of the flexible superfamily Sagenocrinitacea and should not be questioned or apologized for as in Moore (1952) or Lane (1978). Among the Articulata, the Uintacrinida share addition of fixed brachials and interradial plates as a synapomorphy.

Reduction in the complexity of arm branching also occurred in all subclasses. This trend is evident in the evolution of many disparids (Lane & Strimple, 1978), various microcrinoids (Lane & Sevastopulo, 1981, 1982, 1986), and in camerate examples cited below.

Just as the traditional trends do not represent modification from bad to good, these additional trends do not represent modification from good to bad. The morphological trends are more productively viewed as producing different crinoids than better
crinoids. For example, most discussions of evolutionary modification of crinoid filtration fans have regarded the increase in branching density to represent an increased efficiency in feeding. This is probably incorrect in most cases. According to aerosol filtration theory, a filtration fan with an increase in branching density will be adapted to optimally capture food particles of a different size (Rubenstein & Koehl, 1977; LaBarbera, 1978; Meyer, 1979; Ausich, 1980; Kammer, 1985; Kammer & Ausich, 1987). Therefore evolutionary modifications in crinoid filtration fans probably do not allow descendants to occupy their pre-existing niche better but to shift to a new suspension-feeding niche.

The Early Silurian radiation of crinoids provides an instructive example of crinoid evolutionary trends. The Early Silurian crinoid radiation followed the Late Ordovician extinctions that significantly affected stalked echinoderms (Eckert, 1988) and established the morphological and taxonomic character of the Middle Paleozoic crinoid fauna (Early Silurian to late Osagean). Middle Silurian crinoids evolved through a wide range of morphological trends, encompassing both traditional trends and their opposites. In the diplobathrid family Opsiocrinidae, Early Silurian genera evolved by reduction in the number of calyx plates (Silfonocrinus and Rhachicrinus) but subsequent evolution in the family was for a higher bowl-shaped calyx (Ophiocrinus) (Ausich, 1986a). In the Rhodocrinidae (diplobathids), Stereoaster and Xysmacrinus evolved through
addition of plates to the calyx, whereas Krytocrinus displayed a reduction of plates in the CD interradius (Ausich, 1986a).

The evolution of the closely related monobathrid camerate families Glyptocrinidae and Stelidiocrinidae was mosaic in nature with new genera evolving through both an increase and decrease in number of fixed brachials, arms, plates in CD interradius, and number of fixed interscundibrachials within a ray (Ausich, 1985). The Early Silurian monobathrid Manticrinus (Marsupiocrinidae) evolved from Macrostylocrinus and was the immediate ancestor of the middle Silurian Marsupiocrinus (Ausich, 1986b). Manticrinus evolved by a reduction of fixed plates in the calyx, however it gave rise to Marsupiocrinus by an increase in fixed plates. Similarly, the evolution of the Periechocrinidae included both a decrease (Acacocrinus) and an increase (Ibanocrinus) in the number of fixed plates (Ausich, 1987). The successful Middle Silurian Periechocrinus evolved by further addition of fixed calyx plates.

Crinoids must modify their morphology by either the addition or subtraction of plates and/or by size modification of existing plates (Ausich, 1988). Therefore modification of the multielement endoskeletons of crinoids (and all echinoderms) is extremely sensitive to heterochronic changes. Heterochronic processes are very likely the primary controlling factors in the morphological evolution of crinoids. Examples of both paedomorphic and peramorphic processes (McNamara, 1986) have been identified in crinoids (e.g., Broadhead, 1987, 1988, and others),
and the importance of these processes must be explored much more thoroughly. Within a lineage, entire organisms may have been subject to heterochronic change. In addition we must test for the possibility that either parts of organisms are undergoing heterochronic modification or that different parts of an organism are simultaneously undergoing modification due to differing heterochronic processes.

Progress in crinoids takes many forms, but it is only relevant on a local microevolutionary scale.

REFERENCES


RELATIONSHIP OF ANAL SAC SUPPORT AND ARMS
Thomas W. Broadhead
University of Tennessee
Knoxville, TN 37996-1410

It is probably more than conincidental that many early Paleozoic crinoids possessed a prominent series of plates in the anal interray (CD) that at least superficially resemble the adjacent arms. The primanal plate of both diplobathrid and compsocrinid monobathrid camerate crinoids lies within the radial circlet and strongly resembles a radial plate in both size and form. The primanal plate of glyphocrinid monobathrids is usually smaller and displaced upward from the radial circlet. A close association of the primanal with the C ray of camerates is conspicuous in representatives of the diplobathrid genus Pararchaeocrinus, which characteristiclly exhibits a ray ridge extending upward into the anal interradius directly from the C radial (see, e.g., Kolata, 1982:199). The anal X plate of inadunates is intimately associated with the C ray, where it commonly resembles a proximal brachial plate, particularly evident in the Disparida. Similarly, anal X of flexibles is associated with the C ray, particularly in the primitive family Taxocrinidae.

In addition to the close association of the primanal or anal X plate with the C ray in early representatives of crinoids belonging to the three major Paleozoic subclasses, the series of anal plates immediately overlying the anal plate tends to be "arm-like" in appearance in many early or primitive groups. This is true to such a degree in some Ordovician camerates, such as Mecocrinus and Xenocrinus that identification of the anal interray is difficult unless the proximal parts of the fixed arms showing dichotomy or pinnules are also preserved. Such a "differentiated" (with respect to other interradial areas) anal side apparently represents the primitive condition, whereas the "undifferentiated" (i.e. not strongly distinguished from other interradial areas) anal side observed in many glyphocrinids is the derived state in camerates.

"Inadunate" and flexible crinoids also exhibit "arm-like" supports for the anal tube or tegmen. The anal support is a prominent arm-like structure in many species of the Disparida, less commonly in the Cladida (e.g., Rhenocrinacea). Among the disparids, the anal support is commonly prominent along the arm(s) of the C-ray, but in several instances (e.g., the calceocrinids Cremocrinus, Chirocrinus, and Senariocrinus and the eustenocrinid Eustenocrinus) the C-ray superradial supports only the anal X and single series of anal plates. Anal x of Ramseycrinus, one of the earliest crinoids (possibly a disparid), appears to have been supported by highly modified B and D radials (Donovan, 1984). The arm-like anal series of primitive Flexibilia is proportionally much smaller in comparison to the arms than it is in many of the disparid inadunates, and appears to be common only to the Order Taxocrinida.

The close association of the primary support for the anal opening with the arm support of the C-ray, plus the close resemblance of plates of the anal series and those of the proximal parts of the arms in many early Paleozoic crinoids suggests a homologous origin for the primary skeletonized supports of both the food-capturing system and the anal opening. The prominent anal series
would represent a "failed arm" - a homologous structure in terms of skeletal development and origins, but one that never possessed an extension of the water vascular system and thus was incapable of food capture. The fact that branching of the skeletonized part of the feeding support appears to be a response to branching of the water vascular system seems to explain adequately the branching of the arm system, but lack of branching of the anal series. The extreme prolongation of the anal series in many species may be interpreted as closely following the lengthening of the intestine during growth of the crinoid. Thus, the stimulus for addition of additional skeletal elements that were sufficiently robust to act effectively as supports was similarly initiated by growth of tissues belonging to one of the "organ" systems of the crinoid, the water vascular or the digestive.

Additional credence is suggested by the pattern of development exhibited by the digestive system of modern comatulids and its relationship to ontogenetic development of the radial circlct. The digestive tract is relatively well formed in the cystidean stage, but neither an oral nor an anal opening to the outside exists. The terminal end of the intestine extends laterally toward the outer body wall in the area between the basal and oral plates. Only later does the radial circlct of radial plates and anal plate form at this level in the stalked larva. It is suggested that this developmental pattern, in which the extension of the intestine shortly precedes formation of the anal plate, reflects the ancestral state in which plates of the radial circlct were homologous and variously supported extensions of the water vascular and digestive systems.

Generalized evolutionary trends that characterized anal support structures included the suppression of the differentiated anal side in camerates, some disparids and cladids, and the flexibles. In addition, the anal sac of many cladids and modern articulates became less of a heavily plated integral part of the body enclosure. Lane has suggested that the loose attachment of this structure in the last two groups may reflect the modification of the anal sac as a "decoy" to potential predators, but that the anal sac was relatively easily regenerated.
TROPHIC STRUCTURE OF A MIDDLE ORDOVICIAN ECHINODERM COMMUNITY

BROWER, James C., Heroy Geology Laboratory, Syracuse University, Syracuse, New York, 13244-1070, USA.

Two exquisitely preserved echinoderm faunas from the Middle Ordovician (Caradocian Series) Dunleith Formation in the mid-continent of the USA allow unusual insights into the composition of a suspension feeding community that was dominated by stalked echinoderms. The two localities, one from the Rivoli Member near Chatfield, Minnesota and the other from the Sherwood Member at Harmony, Minnesota, are separated by approximately 30 km and are characterized by very similar suites of taxa. The lithologies and stratigraphic and geographic distributions demonstrate that the assemblages were located in a gently agitated area on an equatorial shelf at a depth of approximately 30 to 40 m in the vicinity of the Trans-continental Arch. The area was below normal wave base but well within the reach of storm generated waves. Complete echinoderms are known from three beds in the Rivoli Member, all within 15 cm of a bentonite. The material from the Sherwood Member at Harmony lies in and immediately above a submarine channel. Several processes interacted to rapidly bury and preserve the specimens. Storm deposits are ubiquitous. In one instance, the organisms were overwhelmed by volcanic ash. Fine sediment overlies or underlies the beds with echinoderms, and the animals either sank into the underlying layer or were enveloped by the overlying fine material. Most individuals in the submarine channel appear
to have been detached, transported for a short distance and buried catastrophically. Some specimens rest directly on fine-grained carbonate sediment whereas others are found on top of a layer of disarticulated echinoderm debris derived from individuals that had died previously.

Analogies with modern crinoids yield much information about the life styles of ancient stalked echinoderms. Inasmuch as complete stems are present in all of the common species, the elevations above the seafloor can be reconstructed for the adult crinoids, cystoids and other fixed echinoderms as follows: Ectenocrinus simplex, 25 cm; Cupulocrinus aff. C. gracilis and C. aff. C. conjugans, 13 cm; Abludogyptocrinus aff. A. charltoni, a new genus and species of dendrocrinid, Ptychocrinus n. sp., Carabocrinus n. sp. and Tanaocystis n. sp., five to eight cm; the calceocrinids Cremacrinus guttenbergensis and Calceocrinus gossmani, and Pleurocystites aff. P. squamosus on the substrate. Various other organisms lived on or near the seabed including orthid and strophomenid brachiopods, small twig-like bryozoans, several trilobites and a few asteroids and ophiuroids. Each level is approximately 50 percent below the next higher one. Although the four-tiered structure of the Ordovician animals rivals the complexity known for Mississippian crinoid assemblages, the maximum elevation of 25 cm above the seafloor is considerably less than the 100 cm height reached by Mississippian crinoids.

As with Recent crinoids, the Ordovician crinoids and cystoids are interpreted as passive suspension feeders. During feeding, the arms of extant crinoids are spread at a right angle to the current with the backs of the arms oriented upcurrent. Food particles are caught by the tube-feet as
they eddy around the arms. The width of the food grooves of living and fossil crinoids is proportional to the maximum size of food particles that could be captured. Arm morphology of the various Ordovician forms present at the same level suggests that different food resources were exploited and that different filtration mechanisms were involved in several cases. Recent and fossil brachiopods and bryozoans are also suspension feeders. With respect to the suspension feeders, the primary effect is most likely separation by elevation with secondary division owing to food particle size and filtration mechanism. Feeding habits of the trilobites are more conjectural, but probably involved surface feeding on a variety of food stuffs ranging from organic detritus and micro-organisms to scavenging and predation on small animals. Like similar modern starfish, the asteroids are thought to have been predators. The small ophiuroids were probably microphagous feeders on particles on the seafloor or in the adjacent water column. The overall pattern utilized a wide range of levels and food types and minimized competition between the taxa for food and space.

Only three types of attachment devices are observed in these primitive crinoids, i.e. small terminal holdfasts which were cemented to shells, short distal rootlets penetrating sediment and stem segments which were coiled on the seafloor. In contrast, later crinoids exhibit a larger diversity of attachment modes. The flexible stalk of the recumbent pleurocystitids probably served for crawling and perhaps to temporarily grasp objects on the substrate. A common denominator of the holdfasts in the Ordovician community is that they are restricted to small echinoderms. Attachment devices such as tree stump-like cirrus roots
that are associated with large crinoids are conspicuously absent. This limitation was probably dictated by the nature of the substrate.

The common species are represented by ontogenetic sequences which illustrate the relations between levels inhabited, feeding strategy and relative age. For example, the stem lengths of *Cupulocrinus* aff. *C. gracilis* increase from 8 mm to 13 cm during the observed post-larval growth sequence (cup height from 2.2 to 7.7 mm) so that older animals occupied progressively higher levels throughout ontogeny. Similarly, the average width of the food grooves became wider, ranging from 0.26 mm in youngsters to 0.58 mm in adults. As mentioned above, the width of the food grooves in modern crinoids limits the largest sized food particles that can be processed. Consequently the mature cupulocrinids were able to trap larger food stuffs than the juveniles. The branch density, i.e. number of arm branches divided by area spanned by the arms when feeding, declines from 0.07 to 0.01 throughout development and larger crinoids exhibit arm branches that are relatively more widely separated. On the other hand, the spacing of the adjacent food-catching tube-feet is independent of size and age and was stabilized over an interval of 3.6 to 6.4 tube-feet per mm along one side of the arm. This suggests that these cupulocrinids exploited the same type of food-gathering or filtration strategy regardless of size and age.
THE FUNCTIONAL MORPHOLOGY AND EARLY EVOLUTION OF THE CRINOID COLUMN

Stephen K. Donovan, Department of Geology, University of the West Indies, Mona, Kingston 7, Jamaica.

The crinoid stem has evolved three modes of articulation, the symplexy, the synarthry and the synostosis (Figure 1). All three articulations are known from the Ordovician and thus appeared early in crinoid evolution. By the middle Ordovician articulations had evolved which were essentially almost identical to those of modern isocrinids, millericrinids and bourgueteticrinids, yet variations on the three modes of articulation continued to appear throughout the Paleozoic. Only in the post-Paleozoic articulates did stem morphology apparently become conservative.

The earliest symplectal articulations of probable crinoidal origin are known from the lower Ordovician. It is highly improbable that any crinoid stem was ever muscular (Donovan 1989), so these early stems were, like modern examples, under the active control of mutable collagenous ligaments. The axial canal in these early crinoids varied from narrow to broad, suggesting functional differences. The axial canal of all modern crinoids is narrow and contains mainly nervous tissue. Ancient crinoids with a wide axial canal may have included part of the visceral mass, which later became included in the cup, within the column. Alternatively, it may have been an adaptation to conserve energy, reducing the amount of calcite in the column.

Symplectal articulations prevent the rotation of adjacent columnals, a function performed by ligament fibres alone in synostoses and synarthries. More importantly, the crenulae of symplexes act as guides to facilitate the straightening of the column following curvature. Radial symplexes of circular columnals permit equal
flexibility in all directions. Pentagonal and tetragonal columnals, with symplexie arrayed perpendicular to the sides of the ossicles, are accordingly restricted in their range of flexure directions.

Synostosial articulations are largely limited to some early Ordovician columnals (possibly an artefact produced by poor preservation in at least some cases) and the nodal/infranodal articulation in isocrinids (Breimer 1978: more correctly termed a cryptosymplexy). In isocrinids, such articulations are totally inflexible (unlike apparently similar articulations in the dististele of glyptocystitid rhombiferans) and are planes of autotomy that are regularly spaced down the column. In at least one late Paleozoic crinoid, 'Cyathocrinites' ramosus Schlotheim (Donovan et al. 1986), with only symplexial articulations, it is suggested that constrictions of the axial canal would have enabled autotomy to occur between every pair of columnals with equal facility.

Synarthrial ('see-saw') articulations were developed independently in the column of at least one lineage of every crinoid subclass and in the cirri of comatulids and isocrinids. These cirri contain the only contractile fibres known from the crinoid stem. However, crinoid columns which articulated synarthrially were not adapted for muscular flexure (Donovan 1988, 1989).

The evidence of disarticulated columnals suggests that the Ordovician was a time of 'experimentation', with the evolution of a wide range of functional morphogroups. The majority of evolutionary novelties disappeared at the end Ordovician extinction event. In contrast, the Silurian columnal fauna is morphologically conservative.
References.


FIGURE 1. Schematic diagrams of typical crinoid articular facet geometries (A, C, E) and longitudinal sections through columns (B, D, F) to show the three modes of articulation. A, B, synostosial articulation. C, D, symplesial articulation. E, F, synarthrial articulation. (After Donovan 1989, fig. 1).
Ecogenesis of Post-Paleozoic Crinoids

V.G. Klikushin

Abstract

Seven ecological tiers show to be exist among Post-Paleozoic crinoids: 1 - adhering by the theca basis without stem; 2 - adhering by the distal stem disk; 3 - attaching by the distal radicular cirri; 4 - attaching by the distal anchor; 5 - temporary attaching by the mobil stem cirri; 6 - temporary attaching by the centrodorsal cirri; 7 - no attaching.

Primitive Mesozoic crinoids were stalked. Their stem had a distal disk and reduced proximal cirri (the combination of second and fifth tiers: young Comatulida, Pentacrinida and Encrinida).

First ecogenetic trend consists of the detaching from a distal disk and the development of cirri (the transition to fifth, sixth and seventh tiers) simultaneously with the stem perfection by appearance of the criptosymplectic sutures below nodals (Isocrinidae) or without them (Holocrinidae), simultaneously with the shortening of the functional stem length (Pentacrinidae) by a consolidation of the theca and arms (Tulipacrinidae). The transition to sixth tier is the result of the connection of proximal stem nodals into one centrodorsal (Comatulida from Isocrinidae). The transition to seventh tier is the complete detaching from a stem (Roveacrinida from Tulipacrinidae). Regressive lines are occasional, e.g. transition to second tier (Thiolliericrinidae among Comatulida) and, possibly, to first tier (Pseudosaccocomidae from ?Thiolliericrinidae).
Second ecogenetic trend consists of the attachment by distal stem disk without cirri (second tier: Dadocriinidae) simultaneously with development of a strong stem (Millericrinidae) or with differentiation of a stem functions (Cyrtocrinida). The appearance of radicular cirri is possible (third tier: Bourgueticrinida) but, at the same time, complete detaching from a stem is also possible (seventh tier: Ailsacrinus). In Cyrtocrinida, the stem had a functional importance (second tier: Hyocrinina) or reduced (second tier: Cyrtocrinina; first tier: Holopodina).

First ecological trend included Encrinida, Pentacrinida (with families Holocrinidae, Pentacrinidae and Isocrinidae), Tulipacrinida (Tulipacrinidae and Lanternocrinus), Comatulida (including stalked Thiollicrinidae) and Roveacrinida. The functional and phylogenetic tendency to a free life-style showed here continually. For instance, the appearance of comatulids and roveacrinids; the development of nodal pairs in isocrinid stems; the adaptation to pseudopelagic life-style (Seirocrinus and, partly, Pentacrinus); the transformation of cirrus organs from attaching to swimming (Pentacrinus).

Second ecogenetic trend is peculiar for Millericrinida (including Dadocriinidae and Proisocrinidae), Bourgueticrinida and Cyrtocrinida (with three suborders Cyrtocrinina, Holopodina and Hyocrinina). Free lived forms are uncommon in these groups.

Two named ecogenetic (and phylogenetic) trends were united into one subclass Articulata that shows to be artificial. I propose the first trend (and group) to name as subclass Holocrinoidea and the second one as subclass Dadocriinoidea.

The derivation of both subclasses took place at the Permian
Retecrinus is a distinctive early to mid-Ordovician camerate crinoid that has been traditionally considered to be primitive primarily because of its relatively simple calyx plating arrangement and nonpinnulate arms. It is currently assigned in the "Treatise" along with Gaurocrinus Miller, 1889 to the family Retecrinidae and the superfamily Rhodocrinitacea Roemer, 1855. Retecrinus has few, if any, synapomorphies with "typical" rhodocrinitacid taxa (including Gaurocrinus), however, indicating a more widely separated taxonomic status. The lack of intermediate ancestral forms for either Retecrinus or rhodocrinitacids makes establishment of character polarity difficult but tentative judgments can be made based on other early crinoide (both camerate and inadunate) and the pramaeval crinoid Echmatocrinus Sprinkle, 1973. Among Retecrinus characters which I consider autapomorphic are 1) interbasal and sometimes interinfrabasal gaps (formed by multilimbed extension of primary calyx plates) and 2) a disjunct axial canal system. Presumed plesiomorphies included: uniserial analis, nonpinnulate arms, irregular polyplated distal stalk, synostosial columnal articulations, and polyplated distal adult holdfast. (These characteristics are also found in early inadunate crinoids.) This situation differs from other rhodocrinitacids which have: pinnulate arms, single axial canal, symplectic column articulations, no or cirruse-bearing holdfasts, and solidly plated cups below the radials (no gaps). Retecrinus is considered to represent a sister group to rhodocrinitacids and if this interpretation is correct, is an early lineage from the initial late Cambrian to early Ordovician radiation. Gaurocrinus is not considered to be in the retecrinid lineage and is probably a rhodocrinitacid.
time. The Inadunata crinoids (Amelocrinidae among Poteriocrininae most likely) were probable precursors for both Holocrinidea and Dendrocrinoidea.

Leningrad Mining Institute

199026 Leningrad, USSR
SOME HYPOTHESES CONCERNING FOSSIL CRINOIDs

N. GARY LANE
Department of Geology
Indiana University
Bloomington, IN 47405

PALEOEKOLOGY

Were many Paleozoic crinoids facultative eleutherozoans?

Way back in 1911 Edwin Kirk, in his Ph.D. thesis, proposed that many Paleozoic pelmatozoans had an eleutherozoic habit. He thought that many were not rooted or fixed in one spot during their lifetime, but rather could break free and swim or crawl about. Recent observations from deep sea submersibles prove that some living stalked crinoids do, in fact, crawl and are not fixed to one spot (Messing et al., 1988).

Kirk thought that some Paleozoic crinoids broke loose from their stem upon reaching adulthood and that this explained why so many stems are found without heads attached. He also believed that other echinoderms, notably cystoids and blastoids, may have been eleutherozoic. Living stalked crinoids that move about typically perch on rocks or other objects that elevate them above the sea floor. This attitude may place them advantageously to intercept food-bearing currents. Living crinoids may have inherited this perching habit from their stemmed Paleozoic forebears who used other organisms—large sponges, coral heads, or other projections above a level bottom—as perches.

Careful morphologic studies may shed some light on whether or not specific Paleozoic crinoids could move about. Stemless Paleozoic forms like Agassizocrinus and Edrioocrinus need to be looked at afresh, in light of these new observations. The style of root systems in Paleozoic forms may give some clues as to movement. Radicular cirri may have been spread over the sea floor as fractional stops to drifting, not buried in the sediment as fixed anchors. The living isocrinoids that move about have the runner-prop style of holdfast. Did Paleozoic crinoids with this type of anchor also have similar abilities? Who had this type of holdfast? The types of articulations in the arms may also give clues as to whether or not the arms could be used for crawling or swimming. Arms with muscular articulations, as in advanced poteriocrinoids, are the most likely candidates for such activity. The arms of flexible crinoids, whether muscular or not, may also have functioned in this fashion. Finally, assessment of arm damage and regeneration may give clues as to breakage due to crawling activities.

How did crinoids compete during their growth cycle?

Stemmed crinoids had to be successful animals at all stages of their life cycle in order to survive. This means that a crinoid that developed from a metamorphosed larva that had settled on the sea floor had to compete with a succession of other adult marine animals as it grew to adulthood. This
competition took the form of access to water currents for food and oxygen. When the crinoid was only two to three cm high it was in direct competition with brachiopods, bivalves and other animals that lived just above the sea floor. A few centimeters higher it was in direct competition with branching and fenestrate bryozoans. Still taller forms competed with glass sponges and short-stemmed pelmatozoans—cystoids, blastoids and short-stemmed crinoids.

Any change in adaptive strategies by any of these other groups could have adversely affected stalked crinoids. The ultimate decline in importance of crinoids in the world ocean may have been due to their inability to adapt to increasing competition at all levels of growth. Extinction of major groups may have been related to this successional nature of selective pressures exerted on crinoid populations.

The impetus for eleutherozoic freedom may have come from benefits derived from breaking away from this constant, repetitive competition with a succession of other animals. Interrupting the cycle by abrupt movement up onto perches, by both stemmed and stemless crinoids, may have been a successful evolutionary strategy that ultimately allowed living crinoids to persist, while other crinoids that could not facultatively break away from the succession of growth competition, failed to survive and became extinct.

Were there deep water stemmed crinoids in the Paleozoic?

Today all stalked crinoids are either bathyal or abyssal in their depth distribution. Virtually all Paleozoic crinoids that are known are thought to have lived in shallow water, neritic, environments. How and when did this transition take place? Were there both shallow water and deep water Paleozoic crinoids? If so, is there a fossil record for the latter forms? Did shallow water crinoids get shoved into deeper water in the Mesozoic or Cenozoic eras?, or did stalked crinoids become extirpated in shallow water while they continued to thrive in deeper water. If the latter case is true, when did this change occur?

The recent analysis by Jablonski and Bottjer (1988) involved post-Paleozoic crinoids. However, they lumped together middle shelf, outer shelf, and bathyal occurrences into a single "off-shore" category. While this may be the most refined classification that their data allowed, the fact remains that there are no shelf stalked crinoids alive today, they are all deeper water forms, and the relevance of their analysis is open to question.

CLASSIFICATION AND EVOLUTION

Is the present classification of the Class Crinoidea satisfactory at the family level and at higher levels?

There are numerous problems in the classification of crinoids that reflect uncertainties or misconceptions about the major aspects of evolution within this group of animals.

The Class Crinoidea may not be a natural clade but rather
may be polyphyletic. In contrast, Ausich (1988) indicates that all crinoids share a common bauplan of the calyx.

The several subclasses may not be closely related to each other. For example, the Subclass Camerata has little apparent relationship to the other subclasses of crinoids. The symmetry, cup plate homologies, structure of the tegmen and nature of the arms in camerate crinoids bear little or no resemblance to these features in other Paleozoic forms. There is little indication of a common ancestor for camerates and other crinoids. Consideration might be given to elevating the Subclass Camerata to a separate class, and restricting the name Crinoidea to the other subclasses.

The other subclasses, however, are probably related to each other. The group termed "inadunates" should probably be abandoned or used only in an informal, lower case, way, similar to the way that regular and irregular echinoids are used today. If camerates were excluded from crinoids, then inadunata would essentially be synonymous with Crinoidea. Perhaps several separate but equal subclasses should be recognized, as has been done in part by recent authors (Kelly, 1982, 1986; Ruzhov, 1985; Broadhead, 1988; Donovan, 1988). Such a classification might look like this:

Subclass Echmatocrinacea
Subclass Hybocrinacea
Subclass Dipsarida
Subclass Cladida
Subclass Flexibilia
Subclass Articulata

Groups not covered in such a scheme include the Coronoida (Brett, et al., 1983) and the uniserial, pinnulate Ordovician camerates. This arrangement places emphasis on the early, Ordovician, radiation of subclasses of crinoids that reflects in a minor way the more major radiation of echinoderm classes during that time interval.

The articulate crinoids certainly did evolve from the inadunates in Permian or Early Triassic time, although the details of this transition are poorly understood (Sims, 1988a; 1988b). The features that characterize articulates may have evolved by mosaic evolution from poteriocrinoids. There are Pennsylvanian-Permian families that include forms that have uniserial, pinnulate arms that branch on the second primibrachial and that lack an anal plate in the exterior of the cup. Sims selected the Erisocrinidae of the cladids as an outgroup for comparison with the articulates. While erisocrinids share several features with the encrinoids of the Triassic, they are not nearly as similar to other Mesozoic crinoids as are other Late Paleozoic cladids like the aesiocrinoids, for instance. Sims placed emphasis on the presence of a nerve canal within the calyx plates of encrinoids and used this as basis for placement of this Triassic group in the articulates. However, there are advanced poteriocrinoids in the Pennsylvanian and Permian that have a similar condition of the axial nerves. The presence of biserial arms in the encrinoids is a strong basis for inclusion of these crinoids in the cladids. There is little
evidence available as to when the mouth and proximal ambulacral
grooves became open to the exterior and were no longer submerged
under tegrnal plates. Sims (1988a) states that an open mouth and
proximal food grooves are present in all Mesozoic crinoids and
uses this character as a prime diagnostic feature, but these
features have not been definitely identified on the tegmen of
many Mesozoic crinoids. This must surely be one of the most
important defining characters for the articulatea. Careful study
of European Triassic articulate tegmens may shed some light on
this problem.

Are the cladids a single, coherent evolutionary unit?

The current distinction between dendrocrinoid and
poteriocrinoid cladids is clearly in error and needs to be
emended. The two principal differences between the two groups:
presence or absence of true pinnules, and presence or absence of
muscular arti&ulations between radials and first primibrachials,
are either shared by families and genera now placed in separate
suborders, in the case of pinnules, or have not been certainly
differentiated, as in the case of arti&ulations. A careful
phenetic study of these crinoids, especially currently recognized
genera and families of Devonian and Mississippian ages, needs to
be undertaken. This should be followed by a cladistic
interpretation of evolutionary lineages within these groups.
Adequate character lists need to be developed for these groups as
well as for other groups of crinoids.

Finally, the classification within the poteriocrinoids is
almost certainly in a shambles. The very large number of
Pennsylvanian and Permian genera of advanced poteriocrinoids are
commonly differentiated on the basis of very slight morphological
differences in the dorsal cups. These very carefully
discriminated sets of species need to be tested for their
validity. They may prove to be among the best studied fossil
crinoids known, or they may include many synonyms. Again, careful
phenetic studies of many characters need to be applied to these
fossils in order to determine the taxonomic validity of genera
and families as currently recognized. I predict that such studies
would result in conspicuous revision of these important Late
Paleozoic forms.

How did the comatulid crinoids evolve?

Sims (1988a) has recently addressed the origin of the
comatulid crinoids, the dominant and most diverse group
of living crinoids, that first appear in the Early Jurassic. What
was the ancestral stock for these crinoids? There are two general
possibilities. Sims (1988a) derived the comatulids from the
stalked pentacrinoids by loss of the stem in the adult.
Alternatively the comatulids may have evolved from a group that
already had lost the adult stem, the Order Roveacrinida, which
first appear in the Triassic and have a very patchy
distributional history in the Mesozoic before they became extinct
at the close of the Cretaceous. Sims dismisses the roveacrinoids
as poorly understood. The morphologic features that are judged to
be useful for denoting genetic relationships need to be carefully considered. A cladistic analysis of Mesozoic stalked crinoids, the roveacrinoids and the comatulids should prove useful in helping to resolve this problem.

REFERENCES


Growth rate of stalk of *Metacrinus rotundus* Carpenter and its functional significance

Tatsuo OJI

Geological Institute, University of Tokyo, Tokyo 113, Japan

An attempt was made to estimate growth rate of stalk of a modern stalked crinoid, *Metacrinus rotundus*, using two different methods. One is based on the measurements of oxygen isotopic ratio of the crinoid skeletons. Annual change of water temperature recorded in a series of proximal to distal nodals, is correlated with annual change of water temperature measured monthly near the crinoid habitat. The other method is based on the size distribution of the specimens collected at a station in different seasons. There are clusters in the size distribution, and the difference of the two clusters in the young individuals is tentatively assigned here as corresponding difference of the size of one year. The rate of stalk growth estimated by the former method was 70-80 cm/year, and that by the latter method was 36-54 cm/year. If these results are correct, this species has extraordinarily high rate of stalk growth. Such rapid growth of stalk may be explained as follows: (1) *M. rotundus* is a dweller of high-energy environment, and the distal stalks are often mechanically damaged. Therefore, rapid renewal of such injured
stalk may be necessitated. (2) Isocrinids may be able to autotomize the distal stalk, and in at least some species they can relocate themselves occasionally. Therefore, individual must always possess ample length of stalk, preparing the autotomy. Isocrinidae can be interpreted as a group of stalked crinoids which has succeeded in changing habitats by discarding distal part of the stalk. This way of life is very different from most other stalked crinoids which permanently attach themselves to substrate by the stalk. At least in the case of Isocrinidae, high rate of the stalk growth may explain why only columnals are dominantly found in the geologic record over brachials.
MORPHOLOGIC CHARACTERS USEFUL IN THE CLASSIFICATION OF LATE PALEozoic INADUNATE CRINOIDS

Ronald D. Lewis
Department of Geology
Auburn University, AL 36849-5305

The rapid disarticulation of the inadunate crinoid skeleton has produced the following problems for the crinoid systematist: (1) many taxa are known from one or a few complete or nearly complete crowns, resulting in de facto typologic species concepts, and (2) many taxa are known from only that part of the crown which resists disarticulation the most, the cup. The great diversity of poteriocrinines and repeated convergence and parallelism within the group complicate attempts to determine phylogenetic relationships.

Moore and Plummer (1940, p. 33) state, "Among the characters of the poteriocrinids, the nature of the articular facets and the structure of the arms seem to furnish the soundest approach to a classification that has genetic significance... Attention is directed especially to characters of the articular facet on the radial plates, because such features as relative width and angle of slope appear to be rather definitely associated with certain forms of the dorsal cup that are deemed significant of membership in a given group." This early insight has not been followed as emphasis shifted toward the configuration of the cup.

Reexamination of Sciadiocrinus and its relationship to pirasocrinid genera, consideration of the variability in cup shape in some families (e.g., the Cromycorinidae), and my recent work with separate radial plates from the Wann Formation in Oklahoma support Moore and Plummer's emphasis on articular facets and arm structure, particularly at the family level. Cup shape may be more variable than is generally appreciated. With the increased understanding of the relationship between ontogeny and phylogeny, more growth studies are needed to clarify the systematics of Late Paleozoic inadunate crinoids.

Moore, R.C., and F. B. Plummer, 1940, Crinoids from the Upper Carboniferous and Permian strata in Texas. The University of Texas, Bulletin 3945, 468 p.